

TWO MOUTHPART MODIFICATIONS IN LARVAL NOTODONTIDAE (LEPIDOPTERA): THEIR TAXONOMIC DISTRIBUTIONS AND PUTATIVE FUNCTIONS

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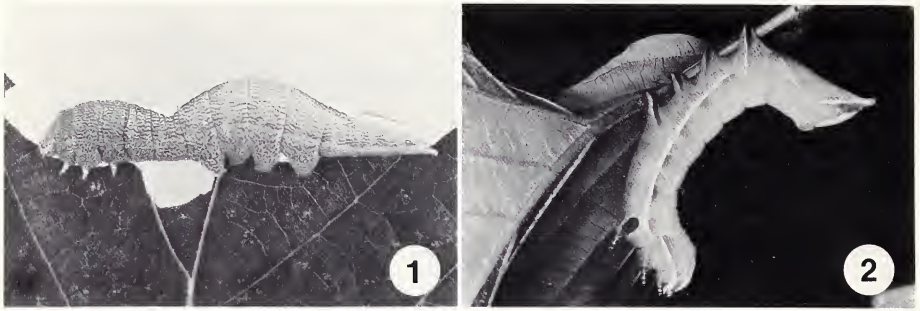
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Abstract.—Two apomorphic features of the larval mouthparts in Notodontidae (Lepidoptera) are described and illustrated, and their taxonomic distribution within the family is documented. One hundred and fifty-four species of notodontid larvae were examined. These represent 90 genera and all currently-recognized subfamilies and tribes. The stipital lobe, a membranous projection on the dorsoposterior portion of the maxillary complex, varies in size and shape but occurs in 143 of the species studied. It does not occur in the Noctuidae, Lymantriidae, or Arctiidae. The majority of notodontid larvae exhibit a distinct developmental change in mandibular morphology, from a serrate cutting edge in first instars to a smooth edge in later instars. A serrate mandible is typical of all instars in other noctuoids. Like the stipital lobe, presence of a smooth mandibular margin is broadly distributed among notodontids. Speculations concerning the functional significance of these mouthpart modifications are presented, and their potential use as synapomorphies for the family is discussed.

The morphology of larval mouthparts has been quite thoroughly studied for the Noctuidae (e.g., Ripley, 1923), and mouthpart characters have been used in systematic papers by numerous noctuid workers (e.g., Crumb, 1929, 1956; Beck, 1960; Chu et al., 1963; Godfrey, 1972; Eichlin and Cunningham, 1978; McCabe, 1988; Merzheevskaya, 1988; Neil, 1988). Mouthparts of larval Notodontidae, in contrast, have rarely been investigated (Gardner, 1943, 1946; Godfrey, 1984; Weller, 1987). In this paper we discuss two modifications found in notodontid larvae.

Grimes and Neunzig (1986) first described a structure, which they termed the stipital lobe, on the larval maxilla of two notodontid species, *Macrurocampa marthesia* (Cramer) and *Schizura unicornis* (J. E. Smith). The lobe is a projection on the stipes which obscures the dorsoposterior aspect of the galea. Grimes and Neunzig (1986) suggested that the stipital lobe may be uniquely derived for the Notodontidae because they did not find it in 23 other ditrysian families.

Macrurocampa marthesia and *Schizura unicornis* are members of the tribe Heterocampini (Forbes, 1948). To better understand the stipital lobe's taxonomic distribution and morphological variation, we examined additional species representing all five subfamilies and seven tribes currently recognized in the Notodontidae, including the Old World Thaumetopoeinae and Neotropical tribe Diopitini, the latter



Figs. 1, 2. 1. *Heterocampa obliqua* Packard, last instar (pinkish brown form) on *Quercus macrocarpa* Michx. (Fagaceae), central Illinois, USA. 2. *Crinodes besckei* (Hübner), last instar (green form) on *Gouania polygama* (Jacq.) Urban (Rhamnaceae), Santa Rosa National Park, Guanacaste Province, Costa Rica.

recently having been reduced from familial to tribal status (Minet, 1983; Weller, 1989).

We also discuss a developmental change in mandibular morphology characteristic of notodontid caterpillars. The mandibles of almost all other Lepidoptera larvae, including noctuoids, bear a series of large teeth along each cutting edge (e.g., see figures in Peterson, 1962; Godfrey, 1972; McCabe, 1988; Neil, 1988). In most notodontids, however, although the mandibles are toothed in first instars, the cutting edges are smooth in succeeding instars (Gardner 1943, 1946; Weller, 1987).

After describing morphological variation in the stipital lobe and notodontid mandible using *Heterocampa obliqua* Packard (Fig. 1) and *Crinodes besckei* (Hübner) (Fig. 2) as examples, we document these character state distributions by examining larvae of 154 notodontid species. Finally, we offer speculations concerning the functional and phylogenetic significance of the two structures.

MATERIALS AND METHODS

Our study was based on alcohol-preserved specimens from the collections of J. G. Franclemont (Cornell University), Susan Weller (University of Texas, Austin), the American Museum of Natural History, the British Museum (Natural History), the Carnegie Museum of Natural History, the United States National Museum, and the Illinois Natural History Survey. Our species sample is broadly representative of the world fauna, and includes taxa from all biogeographic regions.

We follow Forbes' (1939, 1948) tribal and subfamilial arrangement of American notodontid species where possible, but the higher classification of the family is currently rudimentary. Many of the genera we examined, especially from the Neotropics and Old World, have not been assigned to any tribe. The only available treatment for the world fauna (Gaede, 1934) recognized two subfamilies, the Notodontinae (360 genera) and the Pygaerinae (=Melalophinae) (6 genera), and it did not present a tribal classification. Because of these problems, we have simply arranged the genera examined in alphabetical order (Table 1), except that the Thaumetopoeinae and Diopitini are listed separately. We also made detailed examinations of larval mouth-

Table 1. Larval Notodontidae (final instar only) with stipital lobes present (L) or absent (N), and mandibular margins smooth (S) or toothed (T).

Species	Stipital lobe	Mandibular margin ^a	Collection ^b
<i>Afilia oslari</i> Dyar	L	S	JGF
<i>Antheua simplex</i> Walker	L	S	CMNH
<i>Cargida pyrrha</i> (Druce)	L	T	INHS, JGF
<i>Cerura vinula</i> (Linnaeus)	L	S	BMNH
<i>C. sp.</i>	L	S	CMNH
<i>Cerurina marshalli</i> (Hampson)	L	S	BMNH
<i>Clostera albosigma</i> (Fitch)	L	S	INHS, JGF
<i>C. anachoreta</i> (Denis & Schiffermüller)	L	S	BMNH
<i>C. anastomosis</i> (Linnaeus)	L	S	BMNH
<i>C. brucei</i> Hy. Edwards	L	S	JGF
<i>C. curtula</i> (Linnaeus)	L	S	BMNH
<i>C. curtuloides</i> (Erschoff)	L	S	BMNH
<i>C. inclusa</i> (Hübner)	L	S	INHS
<i>C. pigra</i> (Hufnagel)	L	S	BMNH
<i>Cnethodonta griseascens</i> Staudinger	L	S	BMNH
<i>Crinodes besckei</i> (Hübner)	L	T	INHS
<i>Danima banksiae</i> Lewin	N	S	BMNH
<i>Dasylophia abbreviata</i> Schaus	L	S	BMNH
<i>D. anguina</i> (J. E. Smith)	L	S	INHS, JGF
<i>D. thyatiroides</i> (Walker)	L	S	JGF
<i>Datana contracta</i> Walker	L	S	USNM
<i>D. integerrima</i> Grote & Robinson	L	S	INHS, JGF
<i>D. major</i> Grote & Robinson	L	S	INHS, JGF
<i>D. ministra</i> (Drury)	L	S	BMNH, INHS
<i>D. perspicua</i> Grote & Robinson	L	S	USNM, INHS
<i>D. robusta</i> Strecker	L	S	USNM
<i>Desmeocraera ciprianii</i> Berio	L	S	BMNH
<i>D. latex</i> Druce	L	S	BMNH
<i>Didugua argentilinea</i> Druce	L	S	USNM
<i>Drymonia dodonaea</i> (Denis & Schiffermüller)	L	S	BMNH
<i>D. dodonides</i> Staudinger	L	S	BMNH
<i>D. japonica</i> (Wileman)	L	S	BMNH
<i>D. ruficornis</i> (Hufnagel)	L	S	BMNH
<i>Dudusa synopla</i> Swinhoe	L	S	CMNH
<i>Eligmodonta ziczac</i> (Linnaeus)	L	S	BMNH
<i>Ellida caniplaga</i> (Walker)	L	S	INHS, JGF
<i>Epicerura ?amsi</i> Kiriakoff	L	S	BMNH
<i>Epidonta brunneomixta</i> (Mabille)	N	S	BMNH
<i>Epodonta lineata</i> (Oberthür)	L	S	BMNH
<i>Eufentonia nihonica</i> (Wileman)	L	S	BMNH
<i>Euhyparpax rosea</i> Beutenmüller	L	S	JGF
<i>Fentonia ocypete</i> (Bremer)	L	S	BMNH
<i>Furcula bicuspis</i> (Borkausen)	L	S	BMNH
<i>F. bifida</i> (Brahm)	L	S	BMNH
<i>F. borealis</i> (Guérin-Ménéville)	L	S	INHS, JGF
<i>F. cinerea</i> (Walker)	L	S	INHS, JGF

Table 1. Continued.

Species	Stipital lobe	Mandibular margin ^a	Collection ^b
<i>F. furcula</i> (Clerck)	L	S	BMNH
<i>F. scolopendrina</i> (Boisduval)	L		BMNH
<i>Fusapteryx ladislai</i> (Oberthür)	L	S	BMNH
<i>Gargetta ?divisa</i> Gaede	L	S	BMNH
<i>Gluphisia avimacula</i> Hudson	L	S	JGF
<i>G. lintneri</i> (Grote)	L	S	JGF
<i>G. septentrionis</i> Walker	L	S	INHS, JGF
<i>Goacampa variabilis</i> Schaus	L	S	INHS
<i>Harpyia microsticta</i> (Hampson)	L	S	CMNH
<i>H. umbrosa</i> (Staudinger)	L	S	BMNH
<i>Hemiceras nigrescens</i> Schaus	L	S	BMNH
<i>H. sp.</i>	L	S	INHS
<i>Heterocampa guttivitta</i> (Walker)	L	S	BMNH, INHS
<i>H. obliqua</i> Packard	L	S	INHS
<i>H. subrotata</i> Harvey	L	S	INHS
<i>H. umbrata</i> Walker	L	S	INHS
<i>Hippia packardii</i> Morrison	L	S	JGF
<i>Hupodonta pulcherrima</i> (Moore)	L	S	BMNH
<i>Hylaeora dilucida</i> Felder	L	S	BMNH
<i>Hyparpax aurora</i> (J. E. Smith)	L	S	JGF
<i>H. perophoroides</i> Strecker	L	S	USNM
<i>Hyperaeschra georgica</i> (Herrich-Schäffer)	L	S	BMNH, INHS, JGF
<i>Leucodonta bicoloria</i> (Denis & Schiffermüller)	L	S	BMNH
<i>Leucophalera princei</i> (Gündberg)	L	S	BMNH
<i>Liparopsis postalba</i> Hampson	L	S	CMNH
<i>Lirimiris truncata</i> (Herrich-Schäffer)	L	?	SJW
<i>Litodonta hydromeli</i> Harvey	L	S	USNM, SJW
<i>Lobeza suprema</i> Schaus	N	S	BMNH
<i>Lochmaeus bilineata</i> (Packard)	L	S	INHS, JGF
<i>L. manteo</i> Doubleday	L	S	INHS, JGF
<i>Lophocosma atriplaga</i> Staudinger	L	S	BMNH
<i>Macrurocampa marthesia</i> (Cramer)	L	S	BMNH, INHS, JGF
<i>Microphalera grisea</i> Butler	L	S	BMNH
<i>Misogada unicolor</i> (Packard)	L	S	BMNH, INHS
<i>Nadata gibbosa</i> (J. E. Smith)	L	S	INHS, JGF
<i>Neostauropus basalis</i> (Moore)	L	S	BMNH
<i>Nerice bidentata</i> Walker	L	S	BMNH, INHS, JGF
<i>Notodonta dromedarius</i> (Linnaeus)	L	S	BMNH
<i>N. rothschildi</i> Wileman	L	S	BMNH
<i>N. scitipennis</i> Walker	L	S	JGF
<i>N. simplaria</i> Graef	L	S	JGF
<i>Nystalea nyseus</i> (Cramer)	L	S	BMNH
<i>N. sp.</i>	L	S	USNM
<i>Odontosia elegans</i> (Strecker)	L	S	JGF
<i>Oligocentria lignicolor</i> (Walker)	L	S	INHS, JGF
<i>O. semirufescens</i> (Walker)	L	S	USNM

Table 1. Continued.

Species	Stipital lobe	Mandibular margin ^a	Collection ^b
<i>Peridea anceps</i> (Goeze)	L	S	BMNH
<i>P. angulosa</i> (J. E. Smith)	L	S	INHS, JGF, USNM
<i>P. lativitta</i> (Wileman)	L	S	BMNH
<i>P. monetaria</i> (Oberthür)	L	S	BMNH
<i>P. oberthueri</i> (Staudinger)	L	S	BMNH
<i>Phalera bucephala</i> Linnaeus	L	S	BMNH
<i>Pheosia fusiformis</i> Matsumura	L	S	BMNH
<i>P. gnoma</i> (Fabricius)	L	S	BMNH
<i>P. rimosa</i> Packard	L	S	BMNH, INHS, JGF
<i>P. tremula</i> (Clerck)	L	S	BMNH
<i>Psorocampa denticulata</i> Schaus	N	S	BMNH
<i>Pterostoma palpina</i> (Clerck)	L	S	BMNH
<i>P. sinica</i> Moore	L	S	BMNH
<i>Ptilodon capucina</i> (Linnaeus)	L	S	BMNH
<i>P. hoegei</i> (Graeser)	L	S	BMNH
<i>P. jezoensis</i> (Matsumura)	L	S	BMNH
<i>Ptilophora plumigera</i> (Denis & Schiffermüller)	L	S	BMNH
<i>Pygaera timon</i> Hübner	L	S	BMNH
<i>Quadricalcarifera punctatella</i> (Motschulsky)	L	S	BMNH
<i>Q. viridimaculata</i> Matsumura	L	S	CMNH
<i>Q. sp.</i>	L	S	CMNH
<i>Rosema sp.</i>	L	S	BMNH
<i>Schizura badia</i> (Packard)	L	S	USNM
<i>S. biedermani</i> Barnes & McDunnough	L	S	JGF
<i>S. concinna</i> (J. E. Smith)	L	S	BMNH, INHS
<i>S. errucata</i> Dyar	L	S	USNM
<i>S. ipomoeae</i> Doubleday	L	S	BMNH, INHS
<i>S. leptinoides</i> (Grote)	L	S	INHS, JGF
<i>S. unicornis</i> (J. E. Smith)	L	S	BMNH, INHS, JGF
<i>Scrancia stictica</i> Hampson	L	S	CMNH
<i>Seirodonta bilineata</i> Packard	L	S	BMNH
<i>Shachia circumscripta</i> (Butler)	L	S	BMNH
<i>Skewesia angustiora</i> (Barnes & McDunnough)	L	S	JGF
<i>Spatialia jezoensis</i> Wileman	L	S	BMNH
<i>Stauropus fagi</i> (Linnaeus)	L	S	BMNH
<i>Strophocerus pundulum</i> (Schaus)	L	S	BMNH
<i>Suzukiana cinerea</i> (Butler)	L	S	BMNH
<i>Symmerista albifrons</i> (J. E. Smith)	L	S	INHS, JGF
<i>S. canicosta</i> Franclemont	L	S	JGF
<i>S. leucitys</i> Franclemont	L	S	INHS, JGF
<i>Tarsolepis japonica</i> Wileman & South	L	S	CMNH
<i>Tecmessa elegans</i> Schaus	N	S	BMNH
<i>Theroa zethus</i> Druce	L	T	JGF
<i>Torigea straminea</i> (Moore)	L	S	BMNH
<i>Uropyia meticolodina</i> (Oberthür)	L	S	BMNH
<i>Zaranga permagna</i> (Butler)	L	S	BMNH

Table 1. Continued.

Species	Stipital lobe	Mandibular margin ^a	Collection ^b
Thaumetopoeinae			
<i>Anaphe panda</i> (Boisduval)	N	?	BMNH
<i>E. melanosticta</i> (Donovan)	N	?	BMNH
<i>Epicoma tristis</i> Lewin	N	?	BMNH
<i>E. wilkinsoni</i> Tams	N	?	BMNH
<i>Thaumetopoea pityocampa</i>			
Denis & Schiffermüller	N	?	BMNH
<i>Discophlebia catocalina</i> Felder	N	?	BMNH
Dioptini			
<i>Cyanotricha necyria</i> (Felder)	L	T	AMNH
<i>Erbessa glaucaspis</i> (Walker)	L	T	BMNH
<i>Josia auriflua</i> Walker	L	S	BMNH
<i>J. cruciata</i> Butler	L	S	AMNH
<i>J. ligata</i> Walker	L	S	SJW
<i>J. flavissima</i> (Walker)	L	S	BMNH
<i>J. turgida</i> Walker	L	S	BMNH
<i>Phaeochlaena gyon</i> (Fabricius)	L	T	BMNH
<i>Phryganidia californica</i> Packard	L	S	AMNH, INHS, USNM
<i>Zunacetha annulata</i> (Guérin-Ménéville)	L	S	AMNH
Total number of genera examined = 90			
Total number of species examined = 154			

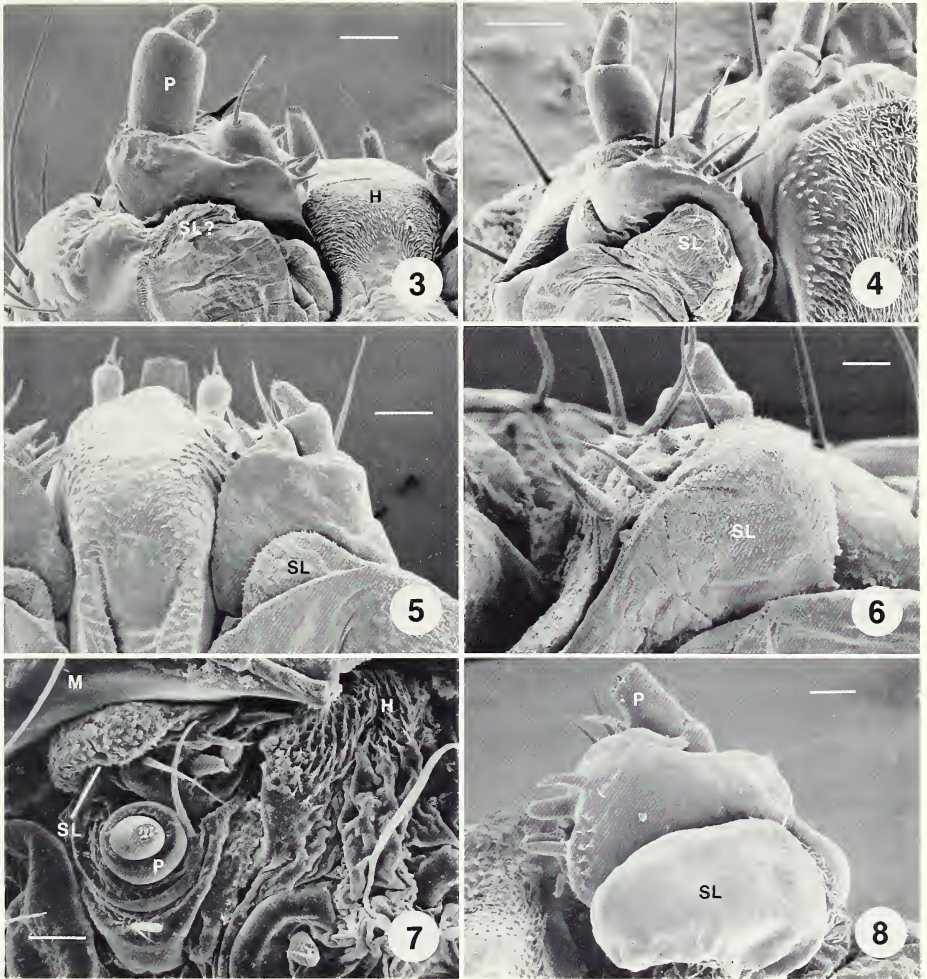
^a In the thaumetopoeines and *Lirimiris*, scored as "?," the mandibles have shallow dentations. These do not easily fit in either of the two categories.

^b Abbreviations: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Carnegie Museum of Natural History, Pittsburgh (CMNH); Illinois Natural History Survey, Champaign (INHS); John G. Franclemont Collection, Cornell University, Ithaca (JGF); Susan J. Weller Collection, University of Texas, Austin (SJW); United States National Museum, Washington, D.C. (USNM).

parts in representatives of the other major noctuoid families, including the Lymantriidae (2 species), Arctiidae (3 species), and Noctuidae (7 species).

Mandibles were removed for study [see Godfrey (1972) for dissection procedure]. Stipital lobes were examined in two ways. All species were studied with dissecting stereomicroscopy while larvae were submerged in 70% ethanol. The lobes were fully exposed by removal of either the mandibles or the entire maxillary/hypopharyngeal complex. The stipital lobe in each of eight species was examined by scanning electron microscopy (SEM). For these, the entire maxillary/hypopharyngeal complex was removed, critical-point-dried, and mounted following the techniques outlined by Grimes and Neunzig (1986). The stipital lobes are membranous, and in some cases they collapsed during preparation; only those that retained their shape are figured with SEM in this paper.

To observe the closing movement of the oral surfaces of the mandibles during adduction, we used 10% potassium hydroxide to clear the heads of last instar larvae of muscle tissue. We then cut away a small, posterior portion of the head capsule



Figs. 3–8. Scanning electron micrographs of last instar larval mouthparts. 3. *Epicoma melanocticta* (Donovan), left maxillary complex (dorsal; scale line = 100 μ). 4. *Clostera albosigma* Fitch, left maxillary complex (dorsal; scale line = 100 μ). 5. *Datana ministra* (Drury), right maxillary complex (dorsal; scale line = 100 μ). 6. *Heterocampa obliqua*, right maxillary complex (dorsal; scale line = 50 μ). 7. *H. obliqua*, right maxillary complex (frontal; scale line = 40 μ). 8. *Phryganidia californica* Packard, right maxillary complex (dorsal; scale line = 40 μ). Symbols: (H) hypopharynx; (M) mandible; (P) maxillary palpus; (SL) stipital lobe.

and inserted microforceps through the enlarged area to grasp the mandibular adductor tendons and simulate the closing process.

RESULTS

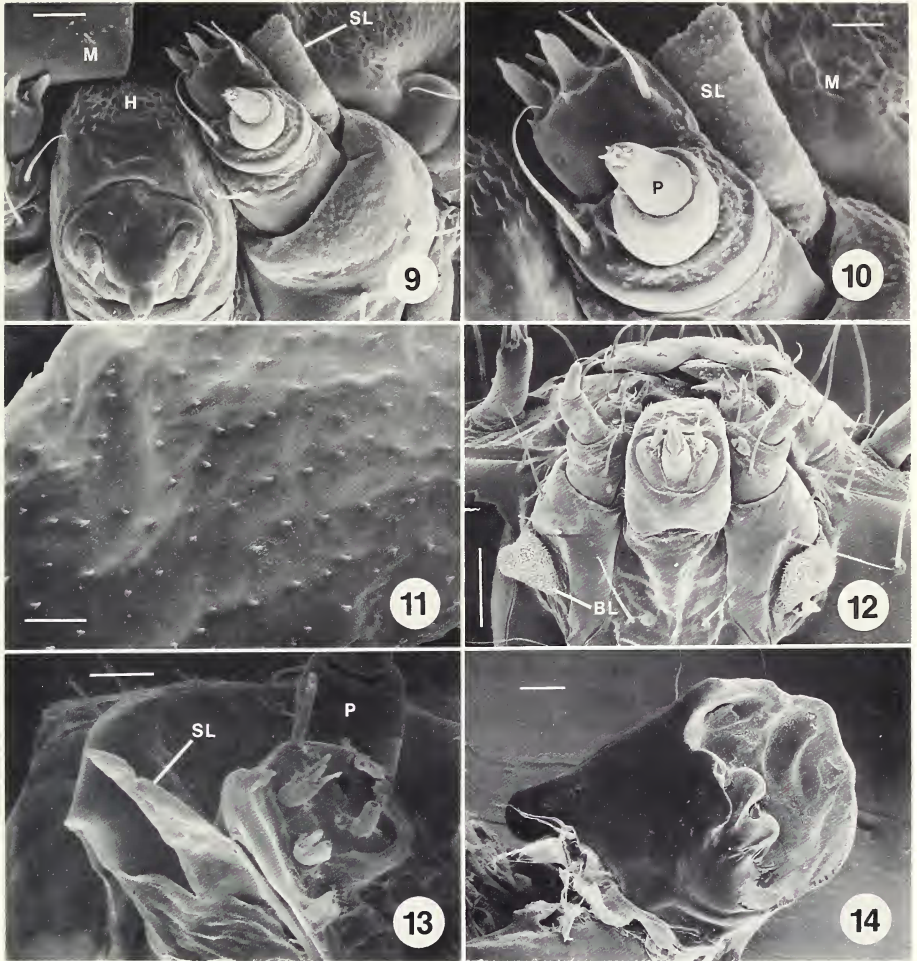
Stipital lobes. Among the notodontid taxa examined, a stipital lobe occurs in 81 of 90 genera (90%) and in 143 of 154 species (92%) (Table 1). It is not found in the other noctuid families we studied (see figures in Grimes and Neunzig, 1986). A small fold occurs on the dorsoposterior portion of the maxillary complex in *Epicoma melanosticta* (Donovan) (Fig. 3), a thaumetopoeine, but we do not consider this to constitute a lobe. There is no trace of a stipital lobe in the other thaumetopoeine genera we studied, *Thaumetopoea*, *Discophlebia*, and *Anaphe*. Five additional notodontid genera lack the lobe.

The size and shape of the stipital lobe varies significantly among Notodontidae. Relatively short, distally-rounded lobes characterize *Clostera albosigma* Fitch (Mela-lophinae) and *Datana ministra* Drury (Phalerinae) (Figs. 4, 5). The large lobe of *Heterocampa obliqua* (Fig. 6), which protrudes slightly from below the ventral margin of the mandible (Fig. 7), is similar to those of the two heterocampines studied by Grimes and Neunzig (1986). The type we observed most frequently has an acute tip, with the lobe often curving dorsally in front of the mandible (Figs. 15, 16). This type occurs in the Gluphisiini, Notodontini, Nystaleini, Hemiceratini, Dioptini (e.g., *Zu-nacetha annulata* Guérin-Ménéville, Figs. 9, 10), and Cerurinae. A lanceolate lobe (Fig. 13) is found in *Goacampa variabilis* Schaus. In still other species, the stipital lobes are greatly swollen and curve upwards so far that they touch the distal margin of the labrum. Such lobes were found in the dioptines *Erbessa glaucaspis* (Walker) and *Phryganidia californica* Packard (Fig. 8), in the Old World genus *Liparopsis*, and in *Nystalea nyseus* (Cramer) (Nystaleini) (Figs. 17, 18). In all cases, the surface of the stipital lobe is spiculate (Fig. 11), and sometimes the spicules are quite prominent (e.g., *Heterocampa obliqua*, Figs. 6, 7). Stipital lobe shape does not appear to vary significantly within genera.

Although stipital lobes can be most easily seen in last instar larvae, they occur in earlier instars as well. The lobes are present from the second to last instars of *Heterocampa obliqua* and *Crinodes besckei*, but SEM revealed that they do not occur in the first instar.

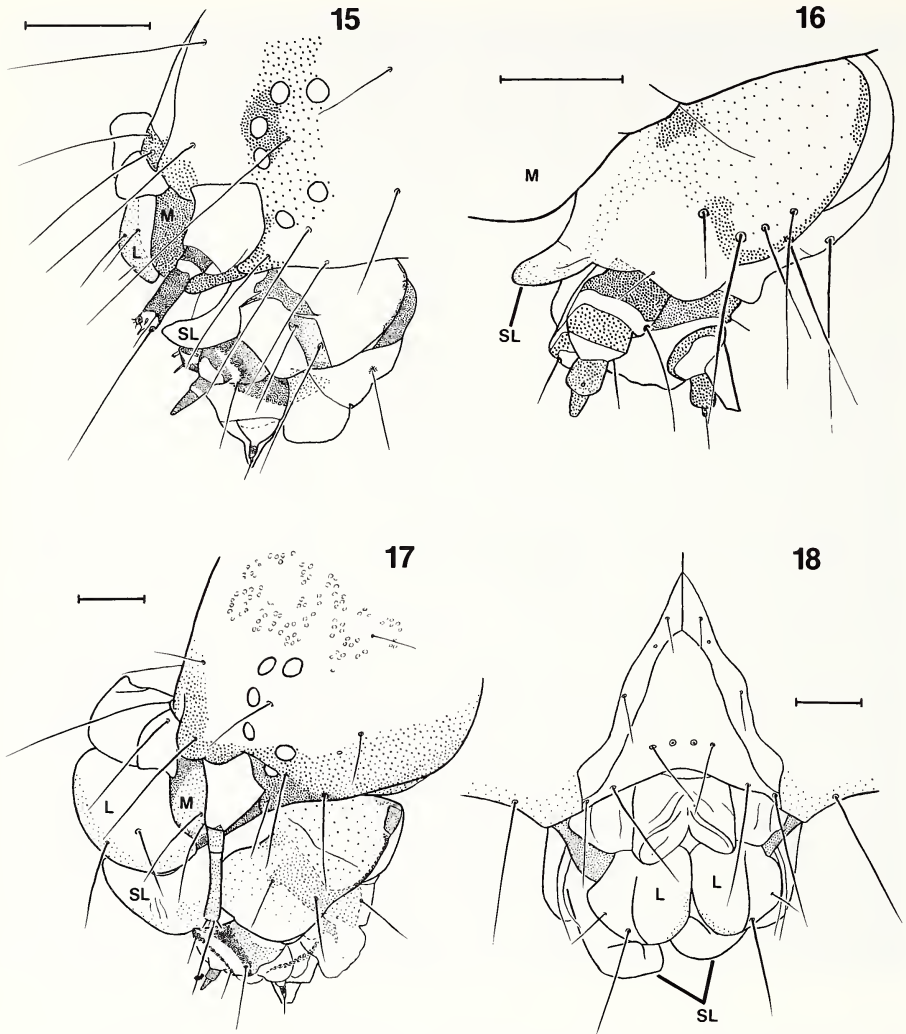
A second type of lobe was observed on the basolateral area of the stipes of *Crinodes besckei* (Fig. 12) and *Nystalea nyseus*. We call this the "basolateral lobe" to reduce potential confusion with the stipital lobe of Grimes and Neunzig (1986). In *C. besckei*, it occurs on the maxilla of the first through fourth instars, but not the last. Early instars of *N. nyseus* were not available for study, but the lobe is prominent in the last instar. The internal morphology and function of the basolateral lobe are currently under study by G. Godfrey, J. B. Nardi, and D. H. Janzen.

Mandibles. The first instar *Heterocampa obliqua* mandible bears five distal teeth and has a weakly concave oral surface with distally extending ridges (Fig. 22). However, as is true for the majority of notodontid species, a dramatic change in mandibular structure occurs during subsequent development. In the second through final instars, the teeth are lost and the distal edge is continuous, except for a slight notch near the dorsal corner. This notch demarks a low, dorsal tooth (Figs. 19–21, 23).



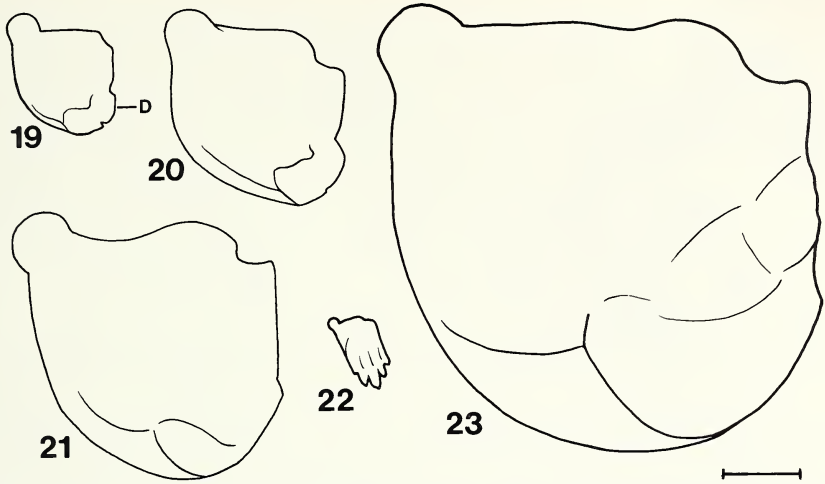
Figs. 9–14. Scanning electron micrographs of larval mouthparts. 9. *Zunacetha annulata* (Guérin-Ménéville), labial and left maxillary complexes (frontal; scale line = 50 μ). 10. *Zunacetha annulata*, left maxillary complex (frontal; scale line = 25 μ). 11. *Zunacetha annulata*, surface of stipital lobe, showing spicules (dorsal; scale line = 10 μ). 12. *Crinodes besckei*, first instar basolateral lobe (fronto-ventral; scale line = 100 μ). 13. *Goacampa variabilis* Schaus (dorsal; scale line = 50 μ). 14. *C. besckei*, last instar right mandible (oral view). Symbols: (BL) basolateral lobe; (H) hypopharynx; (M) mandible; (P) maxillary palpus; (SL) stipital lobe.

Worn mandibles may lack the notch, making the distal edge appear entirely smooth. The series of oral ridges found in the first instar is also lost, being replaced by a single ridge that crosses the mandible between the ventral and distal corners. Associated but less pronounced changes include the following: (1) the adductor apodeme is positioned more distad of the rotational axis than in the first instar; and (2) the mandible protrudes and shows more medial curvature (Figs. 24, 25).



Figs. 15–18. Last instar mouthparts. 15. *Josia flavissima* Walker (lateral). 16. *Phalera bucephala* Linnaeus (lateral). 17. *Nystalea nyseus* (Cramer) (lateral). 18. *N. nyseus* (frontal). Scale lines = 0.5 mm. Symbols: (L) labrum; (M) mandible; (SL) stipital lobe.

A second type of mandibular morphology occurs among notodontids. First instar mandibles of *Crinodes besckei* (Fig. 27) are superficially similar to those of *Heterocampa obliqua*, but in succeeding instars (Figs. 14, 26, 28, 29) they differ in significant ways. The most obvious differences are: (1) the distal, triangular teeth and oral ridges are retained; (2) platelike protuberances appear at the bases of the oral ridges; and (3) there is less mandibular protrusion and a more gradual medial curvature (Figs.

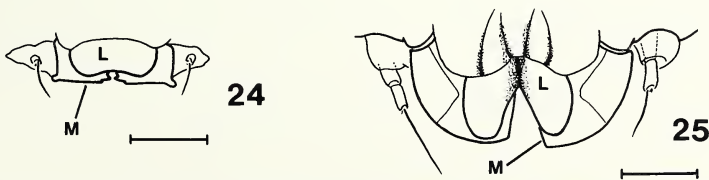


Figs. 19–23. Oral view of left mandibles of *Heterocampa obliqua*. 19. Second instar. 20. Third instar. 21. Fourth instar. 22. First instar. 23. Fifth instar. Scale line = 0.2 mm. Symbol: (D) dorsal tooth.

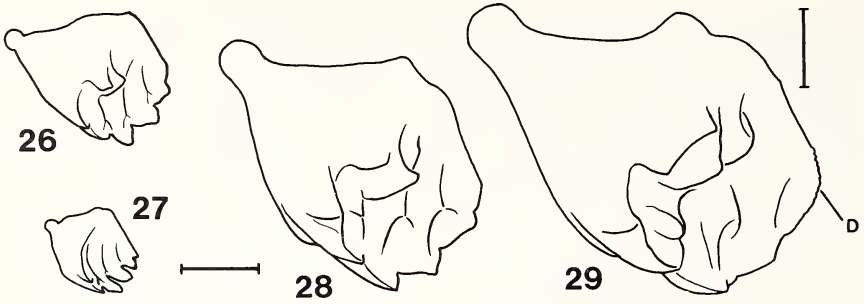
30, 31). In *C. besckei* the oral surface of the mandible becomes progressively more complex with each molt; “pockets” appear below the distal teeth (Fig. 14). These appear to receive the tips of the distal teeth on the opposing mandible (Fig. 32).

DISCUSSION

Mandibular modifications and functions. The teeth on the mandibular margin of first instar *Heterocampa obliqua* caterpillars are first used to chew an escape hole through the chorion, and then to slice and gouge leaf tissue between veinlets on the lower surfaces of fully expanded oak leaves (G.L.G., pers. obs.), leaving the top epidermal layer intact. The skeletonized leaf that results is typical of feeding damage caused by first instar notodontids (Riotte, 1969; Godfrey and Appleby, 1987; Weller, 1987). Later instars clip through the leaf blade, beginning at the outer margin (Weller, 1987). This change in feeding behavior is correlated with loss of the mandibular



Figs. 24, 25. Labrum and mandibles of *Heterocampa obliqua* (frontal view; labral and mandibular setae omitted). 24. First instar (scale line = 0.2 mm). 25. Second instar (scale line = 0.8 mm). Symbols: (L) labrum; (M) mandible.



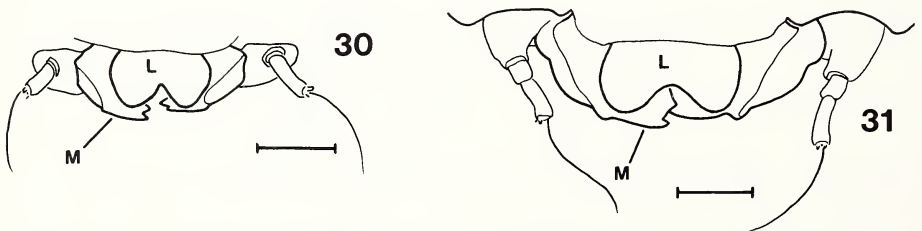
Figs. 26–29. Oral view of left mandibles of *Crinodes besckei*. 26. Second instar. 27. First instar. 28. Third instar. 29. Fourth instar. Scale line = 0.2 mm. Symbol: (D) dorsal tooth.

teeth. Similar changes in mandibular structure were noted by Embree (1958) for larvae of *Psilocorsis faginella* (Chambers) (Lepidoptera: Oecophoridae).

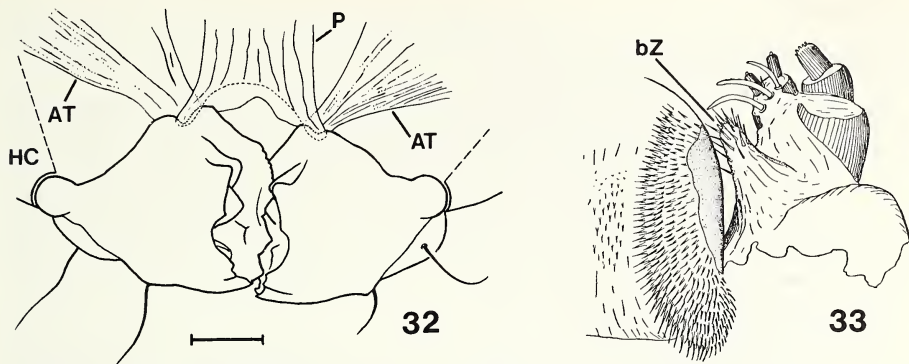
The feeding strategy of *Crinodes besckei* differs from *Heterocampa obliqua*. First instar caterpillars chew completely through the host leaf, *Gouania polygama* (Jacq.) Urban (Rhamnaceae), rather than skeletonizing it. The larva then enlarges the hole. Later instars clip through the leaf, either by chewing through the blade and then moving toward the margin, or by working toward the midrib from the margin. In both cases, larvae tend to avoid primary lateral veins (G.L.G., pers. obs.).

First instar mandibles appear to be incapable of cutting leaf material after it has been removed from the blade. *Heterocampa obliqua* larvae feed on fully expanded oak leaves, which may present a greater ingestive and digestive problem than the tender, terminal *Gouania polygama* leaves on which first instar *Crinodes besckei* feed. By gouging out the softer tissue from oak leaves, first instar *H. obliqua* seem to avoid much of the indigestible material.

Later instars of *H. obliqua* may partially masticate cut leaf tissue by pressing the distal edge of one mandible against the transverse oral ridge of the opposing one, a process observed by Bernays and Janzen (1988) for saturniids. In fifth instars, each mandible has an undulated area proximad of the transverse ridge (Fig. 23). These may have a mashing or crushing function; the surfaces appear to mesh as the mandibles close.



Figs. 30, 31. Labrum and mandibles of *Crinodes besckei* (frontal view; labral and mandibular setae omitted). 30. First instar (scale line = 0.2 mm). 31. Last instar (scale line = 0.8 mm). Symbols: (L) labrum, (M) mandible.



Figs. 32, 33. 32. Mandibles of last instar *Crinodes besckei* in semiclosed position, viewed from the rear through head capsule. Scale line = 0.4 mm. Symbols: (P) pharynx, (AT) adductor tendon, (HC) head capsule. 33. "Beborsteter Zapfen" (bZ) on the maxilla of *Talaeporia tubulosa* (Retzius) (Psychidae), from Dampf (1910).

The mandibular cutting edges of last instar *H. obliqua* and *Crinodes besckei* larvae slide past each other upon adduction. A similar mechanism was described for saturniid and sphingid larvae by Bernays and Janzen (1988). Leaf cutting by saturniid mandibles is scissorlike (Makhotin and Davydova, 1961; Bernays and Janzen, 1988). For *C. besckei*, the initial cut into the leaf blade appears to be facilitated by the serrate dorsal tooth. The dorsal corners of the mandibles are the first parts to meet during biting. The dorsal mandibular serrations illustrated by Bernays and Janzen (1988) may function in the same way. Leaf-edge clipping by the second to fifth instars of *H. obliqua* is theoretically enhanced by the increased distal, linear separation of the adductor apodeme from the rotational axis, and by the more medially-directed cutting edge on each mandible.

In *Crinodes besckei* the plates and pockets proximad of the distal teeth appear to be modified for further mastication of food particles before they enter the gut. When the mandibles close, opposing sets of plates nearly inter-mesh, and opposing teeth insert into the pockets (Fig. 32). These actions parallel the process noted by Bernays and Janzen (1988) for sphingid mandibles. The oral plates may also help retain food particles in the oral cavity and thus assist the hypopharynx during ingestion.

Our observations concerning developmental changes in feeding methods and mandibular morphology of notodontid caterpillars fail to explain why later instars of other noctuoids, most of which clip through the leaf blade while feeding, retain the toothed mandible.

Role of the stipital lobe. Grimes and Neunzig (1986) suggested that the stipital lobes aid the mandibles during mastication. However, because of their membranous nature, the lobes cannot be directly involved in chewing or crushing the leaf. The stipital lobes seem to form seals between the mandibles and maxillae, thereby helping hold leaf tissue within the oral cavity while the mandibles are acting. The large stipital lobes of *Heterocampa obliqua* (Fig. 6) and *Nystalea nyseus* (Fig. 17) may function not only as seals but, in conjunction with the deeply cleft labrum of these species

(Figs. 18, 25), as a channel for the leaf's edge as it nears the mandibles. In first instar *Heterocampa obliqua*, which are leaf skeletonizers, the labrum is barely emarginate (Fig. 24) and the stipital lobe is absent.

Phylogenetic implications. Although the Notodontidae is generally assumed to be a monophyletic group, few synapomorphies are known (Holloway et al., 1987). Perhaps the most frequently cited diagnostic character is the presence of two rather than one middorsal proprioceptor (MD) setae on abdominal segment 1 (A1) of the larva (Hinton, 1946; Common, 1979). However, dioptine larvae exhibit the plesiomorphic condition, a single MD seta on A1 (J. Miller, unpubl. data; Weller, 1989). The only known adult synapomorphy is the presence of a ventrally-directed tympanal membrane (Common, 1979).

The stipital lobe is a uniquely-derived character within the Noctuoidea. Dampf (1910) illustrated a similar structure, which he termed the "beborsteter Zapfen" (Fig. 33), on the larval maxilla of *Talaeporia tubulosa* (Retzius), a primitive psychid (Hinton, 1955), but Dampf's structure is almost certainly not homologous with the stipital lobe. Within the Notodontidae, a stipital lobe occurs in all but 9 of the 90 genera studied (Table 1).

The Thaumetopoeinae, or Thaumetopoeidae of some authors (e.g., Kiriakoff, 1970), contains approximately 100 species, all restricted to the Old World. It is generally regarded as the most primitive notodontid group (Sick, 1940). Based on our examination of six thaumetopoeine species in four genera, the stipital lobe is absent in that group (see Results and Table 1). These findings suggest that the stipital lobe is a derived character supporting the monophyly of a clade which includes all notodontids exclusive of the Thaumetopoeinae. This further supports the hypothesis that thaumetopoeines represent the most basal notodontid lineage.

Relationships among the remaining five genera that lack a stipital lobe, *Danima*, *Epidonta*, *Lobeza*, *Psorocampa*, and *Tecmessa*, are unknown. The first two are Old World taxa (Australia and Africa respectively), while the latter three are Neotropical (Gaede, 1934). Our observations based on general adult appearance suggest that these five genera do not constitute a monophyletic group. However, a test of this hypothesis must await an improved classification for the Notodontidae.

The presence of a smooth mandibular margin in final instar larvae is also taxonomically widespread among the Notodontidae (Table 1). A toothed mandible occurs only in some species of Diopitini, and in four additional genera, including *Crinodes besckei*, as well as two North American species of uncertain placement, *Cargida pyrrha* (Druce) (see also Godfrey, 1984) and *Theroa zethus* (Druce). Further research is required to determine whether these taxa form a monophyletic group. The thaumetopoeine mandible is problematical; it appears to be neither toothed nor smooth, but instead has three or four shallow dentations along its margin. Perhaps this represents a transition state between the toothed mandible of noctuids, arctiids and lymantriids, and the smooth mandible found in higher notodontids. If true, this would imply that the mandibular serrations in species such as *Crinodes* are not homologous with those of other noctuids.

We hope that by describing the stipital lobe and notodontid mandible, we have helped provide two valuable diagnostic features for larvae of the Notodontidae. Furthermore, we hope our research will stimulate future study on the structure and function of noctuid larval mouthparts.

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